

# THE STRUCTURE AND FUNCTION OF THE FACIAL PIT OF THE PIT VIPERS

BY  
WILLIAM GARDNER LYNN

A dissertation submitted to the Board of University Studies of the Johns  
Hopkins University in conformity with the requirements for the  
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Reprinted from THE AMERICAN JOURNAL OF ANATOMY  
Vol. 49, No. 1, September, 1931





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FOURTEEN TEXT FIGURES AND TWO PLATES (SEVEN FIGURES)

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### INTRODUCTION

A striking feature which characterizes one of the important groups of poisonous snakes is their possession of a deep facial pit, situated just in front of the eye. This pit occurs in only a comparatively small number of closely related species and has long been used as a diagnostic character, the family Crotalidae being divided into two subfamilies: the Crotalinae, or pit vipers, in which the pit is present, and

<sup>1</sup> This paper was submitted to the Board of University Studies of the Johns Hopkins University in conformity with the requirements for the degree of doctor of philosophy. The author desires to express his appreciation to Dr. R. P. Cowles for suggestions and assistance, both during the course of the investigation and in the preparation of the manuscript. The photographic work was performed by Dr. C. E. Abromavich, Jr., and Mr. William L. Doyle, for whose help I am most grateful. For aid in obtaining material for this study I wish to extend my thanks to Dr. Howard A. Kelly; Dr. Leonhard Stejneger, of the United States National Museum; Dr. H. Fox, of the Zoölogical Society of Philadelphia, and Mr. R. H. Hutchison, of the Antivenin Institute of America.



the Viperinae, or true vipers, in which it is absent. However, this seemingly unimportant depression in the skin has attracted considerable interest quite aside from its taxonomic utility, for it must be noted that the pit is not simply an anatomical peculiarity of the soft parts, but that it extends also to the hard parts, there being a deep fossa in the maxillary bone in that region. This fact, together with certain other structural details which will be considered later, leads one to conclude that the facial pit is not merely a superficial morphologic peculiarity of these snakes, but is indeed a highly specialized organ with a function which must be of considerable importance to the animal. Early herpetologists engaged in considerable speculation as to the probable function of the pit long before any attempt was made to investigate its anatomy. In the earliest accounts a number of traveler-naturalists in describing crotaline snakes confused the pit with the nostril; but others, who made more careful observations, recognized it as a distinct organ. Some of these regarded it as an external auditory opening, while some attempted to homologize it with the closed nostrils of fishes.

Because of the fact that pit vipers are found only in America and certain parts of Asia, few specimens were available for study by European scientists until comparatively recently. Probably the earliest recorded dissection is that made by Tyson in 1682, who, in the course of his examination of a rattlesnake which he had obtained, noticed the pits and described them briefly. No other investigator seems to have given any attention to the organ until over one hundred years later, when Lacépède (1789), in his "*Histoire Naturelle*" (T. 1, p. 359), again advanced the idea that the pit may be an external auditory opening and recommended the problem for further investigation. In 1804, Russel and Home attempted to make a somewhat more detailed examination of the subject and published a short account of the anatomy of the pits of the fer-de-lance (*Bothrops atrox*) and of several other pit vipers. In this connection, they called attention to

the so-called 'tear-sacs' of deers which occupy a position similar to that of the preorbital pits, and are evidently of a secretory nature; these they believed might be analogous in function to the organ under consideration. In addition, these workers described an oval cavity which, they said, is situated between the eye and the facial pit and has an opening at the corner of the orbit. This was the first mention of a part of the organ which is now known to be of considerable importance, but because their description was incomplete and somewhat erroneous, the significance of the discovery was not realized either by them or by later investigators. The conclusion which Russel and Home drew with regard to the organ as a whole was that it may function as an apparatus for washing the cornea. "These cavities," they said, "must be considered as reservoirs for a fluid which is occasionally to be spread over the cornea; and they may be filled by the falling of the dew, or the moisture shaken off from the grass through which the snake passes."

In 1824, Desmoulins showed that one very important feature of the pit organ had been passed over by the earlier workers in forming their theories. They had failed to observe, or had dismissed as unimportant, the fact that the facial pit is richly supplied with nerves. Desmoulins, stressing this surprisingly large nerve supply, concluded that the organ is sensory in function, and expressed the opinion that it probably functions in olfaction. This contention he based upon the fact that a part of its nerve supply is derived from the ophthalmic branch of the trigeminal nerve. Magendie, a short time before this, had attempted to demonstrate that this branch in mammals serves as a supplementary olfactory nerve; that is, that if the first cranial nerve is cut and the ophthalmic branch of the trigeminal is left intact, olfaction is still possible. This idea, however, is not now accepted and consequently Desmoulins' theory is left unsupported.

A quite different view as to the function of the facial pit is advanced by Harlan (1835), who, noting the close prox-



imity of the pit to the poison duct, regards it as a means of permitting air to act upon the secretion so as to change its chemical properties. Maximilian Prinzen zu Neuwied (1825) had a similar notion, for in speaking of the pit he says, "doch muss dasselbe wahrscheinlich mit dem Giftapparat in Verbindung stehen, da es allen unschädlichen Schlangen fehlt."

Owen ('66), in his "Anatomy of Vertebrates," seems to have disregarded all earlier work on the subject and mentions the pits in *Crotalus* and *Trigonocephalus* as 'secreting follicles.' The same idea was evidently shared by Brühl ('88).

In 1868, Leydig, in his memoir "Ueber Organe eines sechsten Sinnes," devotes a few pages to a discussion of the facial pit and gives an account of his dissection of the pits of three specimens. It seems clear from his statements that Leydig classes this organ among his 'organs of a sixth sense' not because of any essential similarity which it bears to the other sense organs he had described in this connection, but only because of its problematical nature. "Da nun," he says, "nicht daran gedacht werden kann, der Grube die Deutung von Nase oder Ohr beizulegen, so wird man den 'Schleimcanälen' sie anzuschliessen sich berechtigt fühlen dürfen." He himself, of course, fully realized the inconclusive nature of the accounts which had been given up to that time and he expressly recommended the problem to the attention of North American zoölogists who would be in a position to work with fresh material.

The pit organ is again described by Hoffman ('90) in Bronn's "Thier-Reichs," but the description is evidently taken entirely from Leydig. Stejneger ('93) also considers the subject and presents a complete review of the work which had been done on it up to that time.

The most comprehensive investigation of the structure of the organ is that made by West ('00). A number of preserved specimens of pit vipers were studied both by means of dissections and microscopic preparations and the author



was led to believe that this is undoubtedly a sense organ. But he ventured no opinion as to the nature of the stimuli it is designed to receive.

Since that time no further work has been done on the problem from an anatomical standpoint. Chabanaud ('24) gave a short account of some experiments which he thinks give an indication that the pit may have a tactile function. However, the results which he obtained furnish so slight a basis for such a conclusion as to be inconsiderable.

Thus it will be seen that our knowledge of the structure of the pit organ is very fragmentary, while any evidence as to its function is entirely lacking. This is attributable chiefly to the fact that in all the work which has been done on the subject, alcoholic specimens have been used. These were in many cases poorly preserved and were certainly not well adapted for histological study. Moreover, aside from that, the lack of an adequate number of specimens has been a serious handicap, for all the investigators who have taken an interest in the problem have worked in Europe, where these snakes are not found and are therefore available only in small numbers. Since this is so, it is not surprising that conflicting accounts of even gross anatomical features have been given.

It must be added that, while the presence of facial pits is confined entirely to the Crotalinae, yet there are, in certain others of the Ophidia, organs which are somewhat analogous to them in appearance and innervation, although not in position. These are the so-called 'labial pits' of some pythons and boas. They are found in all of the upper labial scutes of some species, while in others they are confined to only a few of the upper labials. In still others they are present in certain of the lower labials. The structure of these pits seems never to have been investigated, but they are believed by Owen ('66), Gadow ('01), and others to be analogous in function to the facial pits of the pit vipers.

In the present study an attempt has been made to work out in detail in a single species (*Agkistrodon mokasen*) the

anatomy, histology, and embryology of the preorbital pit, supplementing this investigation by the study of these same features in a number of other species. Certain of the pythons and boas have also been investigated in order to ascertain the anatomical relations of the labial pits in these snakes, for the purpose of comparing them with the sensory pits of the true pit vipers.

#### MATERIAL AND METHODS

As has been stated, the animal used for the main part of this study is the copperhead snake (*Agkistrodon mokasen*). The material was collected by the author, chiefly in Stafford County, Virginia, where this snake is quite common. The copperhead lives usually on rocky hillsides or near the borders of streams. Abandoned sawmill sites where piles of rotting slabs and sawdust have been left are also very favorable collecting grounds. During the summers of 1927, 1928, 1929, and 1930, some sixty specimens were collected in the above-mentioned region; a few of these were killed and dissected in the field, but most were brought into the laboratory, where they were kept alive until it was convenient to use them. In this way it was possible to use various methods of fixation and preparation which would have been impracticable with preserved specimens. No difficulty was experienced in keeping the animals alive and in good condition in the laboratory. They were kept in large wire-covered wooden boxes, two or three in a box, and were fed at rather infrequent intervals with small rodents and frogs.

The snakes were killed by the use of either chloroform or ether and were then used for dissection or for histological study. All dissections were carried out under the binocular microscope. In preparing the microscopical material use was made of a number of different methods of fixation, staining, etc., which will be described in detail in the section dealing with that phase of the work.

During the course of numerous dissections a number of animals were obtained which contained embryos in different



stages of development. These were fixed in various fixing fluids for later use in the embryological study and a fairly complete series was thus obtained.

In addition to *Agkistrodon mokasen*, a number of other preserved pit vipers were used; namely, *Agkistrodon rhodostoma*, *Agkistrodon piscivorus*, *Sistrurus miliaris*, *Sistrurus catenatus*, *Trimeresurus wagleri*, *Crotalus exsul*, and *Bothrops atrox*. All of these were obtained through the courtesy of the United States National Museum and of the Johns Hopkins University. From the same sources came specimens of *Python reticulatus*, *Python sebae*, *Python molurus*, and *Corallus canina*. Preserved specimens of the Indian cobra (*Naja naja*) and of the banded krait (*Bungarus faciatus*) were obtained through the kindness of Dr. H. Fox, of the Zoölogical Society of Philadelphia.

For comparative embryological study a series of embryos of the water moccasin (*Agkistrodon piscivorus*) was purchased from the Southern Biological Supply Company, of New Orleans, Louisiana.

#### ANATOMY OF THE FACIAL PIT

The gross anatomical details of the pit are best worked out by dissection under a low-power binocular microscope. Formalin-preserved specimens prove most favorable for such a study, since those fixed in alcohol are often poorly preserved, especially with respect to the nervous tissues.

Although the facial pit is always situated in the region between the nostril and the eye, the position of the external opening varies somewhat in different species; in some it is on a direct line between the eye and nostril, in others it is considerably lower. The relation of the pit to the scales of the head is also variable. In order to illustrate these features, drawings of the heads of two crotaline snakes are given herewith (figs. 1 and 2). Excellent illustrations showing the same relations in other species may be found in Garman ('83), Cope ('93), van Denburgh ('22), and other systematic works dealing with the group. It will be seen

from the figures that the pit is widely open anteriorly, but narrows somewhat toward the eye, and is connected with the anterior border of the orbit by a deep groove. The surface of this groove is traversed by many ridges and, in most species, it is more or less completely roofed over by the projecting edges of scales which border it. Thus, in reality it constitutes a closed canal, opening anteriorly into the pit and

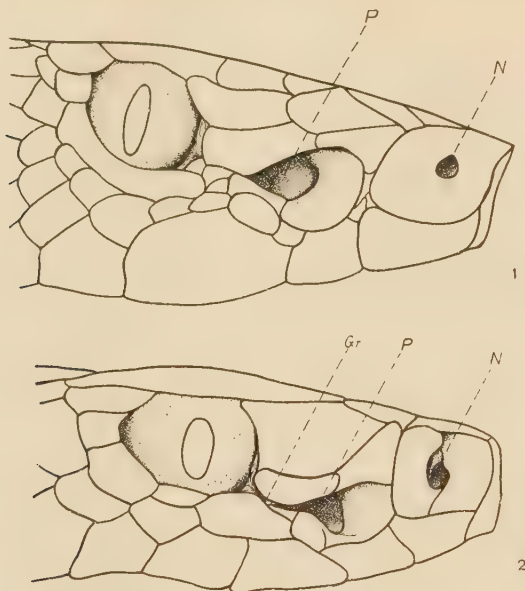


Fig. 1 Outline drawing of the head of *Trimeresurus wagleri* to show the location of the facial pit. *P*, facial pit; *N*, nostril.

Fig. 2 Outline drawing of the head of *Sistrurus miliaris*. *P*, facial pit; *N*, nostril; *Gr.*, groove running from the facial pit to the orbit.

posteriorly into the cavity around the eye. In some species, however, this canal appears not to be roofed over, but is widely open, as in the case of *Agkistrodon strauchii* described and figured by Barbour ('26). Just ventral to the point where the groove reaches the orbit, there is in the skin a small opening or pore which, when probed, is found to lead into a cavity lying directly beneath the floor of the pit itself. It is the floor of this internal cavity which rests in the hollowed-out



portion of the maxillary bone. These relations may be made clear by means of a diagram of a section taken through the head in a horizontal plane (fig. 3). Here we see that the floor of the pit proper constitutes a thin membrane (*p.m.*); this is subtended by an extensive cavity (*I.C.*) whose only communication with the outside is through the small opening (*o.i.c.*) at the border of the eye. This opening is surrounded by a sphincter muscle and is capable of considerable dilatation, but is usually found to be tightly closed. The presence of the inner cavity and its communication with the exterior

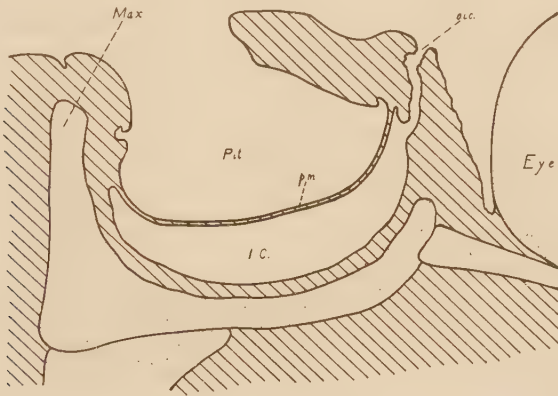


Fig. 3 Diagrammatic horizontal section through the head in the region of the facial pit. *I.C.*, inner cavity of the pit; *o.i.c.*, external opening of the inner cavity; *p.m.*, pit membrane; *Max.*, maxillary bone.

is quite clearly demonstrable upon dissection and it is surprising that it escaped observation for a very long time. Russel and Home, as has been mentioned, undoubtedly noted it, but failed to ascertain its anatomical relations correctly, since they describe it as lying between the pit and the eye and as having no direct relation to the pit. Desmoulins, although his work is otherwise quite admirable, seems to have missed this point entirely. Leydig detected the presence of the inner cavity, but did not investigate it because he regarded it as an artifact caused by faulty preservation. This portion of the pit organ was thus either undiscovered

or wrongly interpreted by all the earlier workers until West ('00) gave a correct description of it. He also called attention to the fact that the 'pit membrane' which is stretched above the inner cavity is probably the chief sensory portion of the organ, since it receives most of the nerve supply reaching the pit. His description of this innervation is, however, not detailed.

Desmoulins (1824) was the first to mention the innervation of the facial pit. He called attention to the fact that the nerve supply is derived entirely from the fifth cranial nerve, the major portions of both the ophthalmic and supramaxillary branches of that nerve being concentrated in this limited area in a way which is not found in any other animal. In order to make clear how important is the change in distribution shown by the trigeminal nerve in these snakes, it will be necessary first to describe briefly the course of the trigeminal in snakes in which the preorbital fossa is lacking.

Comparatively little work has been done on the cranial nerves of any of the snakes. The description found in Bronn's "Thier-Reich" ('90) applies in the main to the python and is derived chiefly from Vogt ('39 and '40). General accounts of considerable value are also found in the works of Fischer ('53), Gaupp ('88), Swan ('64), and others.

In pitless snakes the trigeminal, while still inside the skull, divides into three main branches: 1) the ophthalmic branch, 2) the supramaxillary branch, and, 3) the inframaxillary branch. The first of these, the smallest of the three, does not immediately emerge from the skull as do the others, but runs forward along the floor of the cranium until it reaches the orbit; here it leaves the skull and passes behind the eye, crossing over the oculomotor and optic nerves and running through the substance of the harderian gland. At the dorsal anterior corner of the orbit it enters a foramen between the frontal and palatine bones and, running close to the olfactory nerve, finally becomes distributed to the skin above the nostril and at the tip of the muzzle.



The supramaxillary branch of the trigeminal divides before leaving the skull into two branches, a small dorsal and a large ventral one; these emerge together through a foramen in the pro-otic. The dorsal branch again divides, sending branches to the skin at the corner of the eye and to the masseter and temporal muscles.<sup>2</sup> The ventral branch runs anteriorly and ventrally, passing over the pterygoparietal muscle and giving off a small thread to the poison gland. Upon reaching the orbit, it divides into two branches. The smaller of these runs superficially under the edge of the eye and, at its anterior ventral border, turns ventrally so as to reach the upper lip beneath the nostril; here it passes inward and ramifies to supply the roof of the mouth in that region. The larger branch of the supramaxillary dips down under the ectopterygoid bone and, entering the orbit, runs under the eye along the pterygoid bone, giving off along its course several small branches to the upper lip. A number of delicate communicating branches connect it with the sympathetic system. Upon reaching the maxillary, the nerve enters a foramen in that bone and, passing through it, divides into two parts. One of these ramifies in the skin of the central part of the roof of the mouth, while the other passes anteriorly, finally ending in branches at the base of the snout.

The inframaxillary branch of the trigeminal leaves the skull by a separate foramen and runs ventrally to supply the lower jaw. It takes no part in the innervation of the facial pit and so will not be considered here.

Let us now consider the course of the trigeminal in the pit vipers. The description which will be given is based upon dissections of a number of freshly killed or formalin-preserved specimens of the copperhead. Figures 4 to 8 are drawings showing successive stages in the dissection. In this snake, as in others, the trigeminal gives rise to three main branches. The ophthalmic branch, as in other snakes, runs forward inside the skull, penetrates into the orbit, and after

<sup>2</sup> With respect to musculature, the nomenclature used by Hoffmann in Bronn's "Thier-Reich" (1890) has been followed.

traversing it reenters the skull at the junction of frontal and palatine. Now, however, it divides into two branches: a small dorsal one which goes to supply the skin of the snout, and a much larger one which runs ventrally just under the skin and furnishes the nerve supply for the dorsal portion of the facial pit (figs. 4 to 7, *V1*).

The supramaxillary branch gives off the usual small branches to the skin and to the masseter and temporal

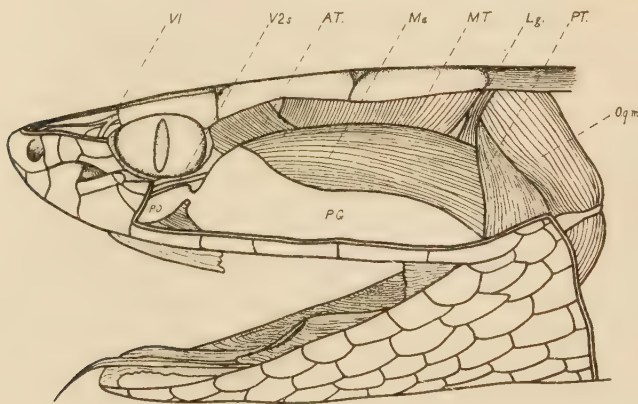


Fig. 4 Side view of the head of *Agkistrodon mokasen* after removal of the skin. *V1*, ophthalmic branch of the trigeminal nerve; *V2s.*, superficial branch of the superior maxillary branch of the trigeminal; *P.D.*, poison duct; *P.G.*, poison gland; *A.T.*, anterior temporal muscle; *M.T.*, middle temporal muscle; *P.T.*, posterior temporal muscle; *Ma.*, masseter muscle; *O.q.m.*, occipito-quadrato-mandibular muscle; *Lg.*, ligament connecting poison gland and skull.

muscles and another small branch which supplies the poison gland (fig. 5). The main portion, however, runs down over the pterygoparietal muscle (fig. 5, *P.p.*) and under the anterior temporal muscle (fig. 5, *A.T.*). It now divides into two main branches, one of which passes above the transverso-maxillo-ptyerygo-mandibular muscle (figs. 5 and 6, *T.m.p.m.*), while the other dips down to pass under this muscle. The first-mentioned branch is the smaller of the two; it runs forward superficially along the ventral border of the eye (figs. 4 to 6, *V2s.*). Under the anterior portion of the eye two thin

threads are reflected toward the border of the upper lip, but the main portion of the nerve breaks up into six or seven branches, all of which are distributed to the ventral posterior part of the pit.

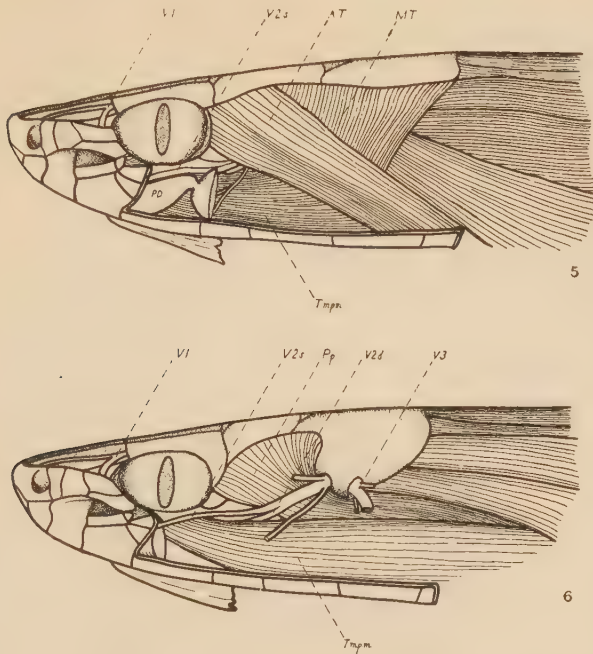


Fig. 5 Side view of head of *Agkistrodon mokasen* after removal of the poison gland and the masseter, posterior temporal, and occipito-quadrato-mandibular muscles. Lettering as in the preceding figure. *T.m.p.m.*, transverso-maxillo-ptyerygo-mandibular muscle.

Fig. 6 Side view of the head of *Agkistrodon mokasen* after removal of the anterior and middle temporal muscles. Lettering as in preceding figures. *V2d.*, deep branch of the superior maxillary branch of the trigeminal; *V3*, inferior maxillary branch of the trigeminal; *P.p.*, pterygo-parietal muscle.

The larger branch of the supramaxillary dips down under the ectopterygoid and runs along the pterygoid bone (fig. 7), thus coming to lie behind the eye. Anteriorly it passes along the inner border of the maxillary bone, finally reaching a foramen near its anterior edge (fig. 8). Here a small branch is given off which runs forward to the roof of the mouth.



The larger branch of the nerve, however, passes through the foramen and breaks up in branches in the anterior part of the facial pit.

Briefly, then, it may be said that, in snakes having no pits, the trigeminus supplies the skin of the face and roof of the

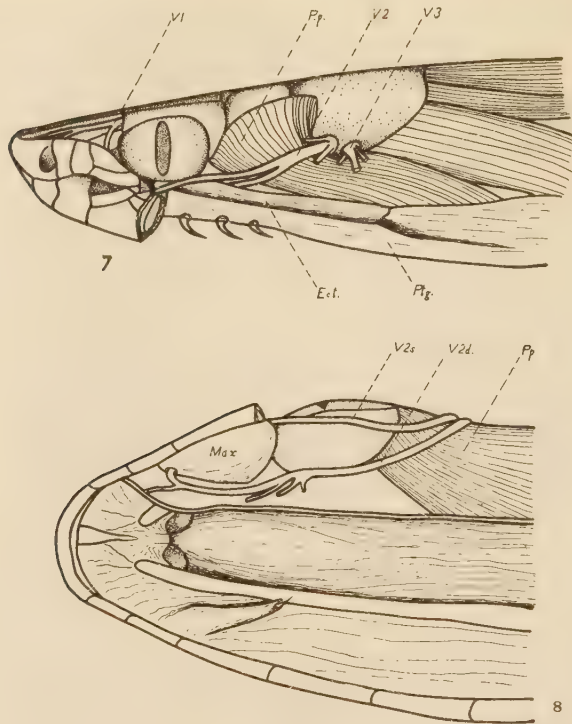


Fig. 7 Side view of the head of *Agkistrodon mokasen* after removal of the transverso-maxillo-pterygo-mandibular muscle. Lettering as in preceding figures. *Ect.*, ectopterygoid bone; *Ptg.*, pterygoid bone.

Fig. 8 Ventral view of the dissection shown in figure 7 after removal of the pterygoid and ectopterygoid bones. Lettering as in preceding figures.

mouth together with certain of the muscles. Its fibers, which supply nerve endings in the skin, are believed to be chiefly sensory in nature, probably functioning mainly in the perception of tactile stimuli. In the pit vipers, on the other hand, by far the major portion of both the ophthalmic and supramaxillary branches of the trigeminal goes to supply the

pit, furnishing this organ with a nerve supply which is comparable in amount to that of any of the sense organs of the head.

To give an idea of the ultimate distribution of these nerves in the pit itself, it will first be necessary to consider the detailed anatomy of that organ. As has been stated, there is beneath the pit a second cavity which lies between the pit and the maxillary bone and communicates with the exterior through a small opening near the eye. This inner cavity is separated from the cavity of the pit proper by a very thin membrane, as illustrated in the diagram (fig. 3), and the walls of the inner cavity as well as those of the outer are covered by a horny cuticle continuous with that which covers the rest of the body. The 'pit membrane,' therefore, has both its inner and outer faces covered with cuticle. Between these two cuticular layers there is a very thin and transparent sheet of tissue which is made up of but a few layers of cells, and it is in this sheet that the ultimate branches of the nerves supplying the pit are distributed. In order to demonstrate the distribution, the following method was used: The organ was dissected away from the maxillary bone, care being taken to avoid cutting into the inner cavity whose inner wall is separated from the maxillary by only a thin layer of connective tissue. The specimen was then pinned, skin down, in a dissecting dish and the fine nerve branches were dissected out. These nerves run to the edges of the pit and then seem to end abruptly, due to the fact that, instead of running along the inner wall of the inner cavity, the nerves penetrate through it and spread out in the pit membrane. This becomes at once apparent if the inner wall of the inner cavity is removed. Then the pit membrane is seen from the inside and, since it is so thin as to be almost transparent, the nerves entering and repeatedly branching in it are easily seen (fig. 9). The histological details of these nerve endings will be discussed at length in the next section.

## HISTOLOGY OF THE FACIAL PIT

The histological details of the structure of the facial pit are almost entirely unknown, for only two investigators have given any attention whatever to these features. Leydig ('68) briefly described the ending of the nerves in the pit and figured certain 'Terminalganglienzellen' with which he believed

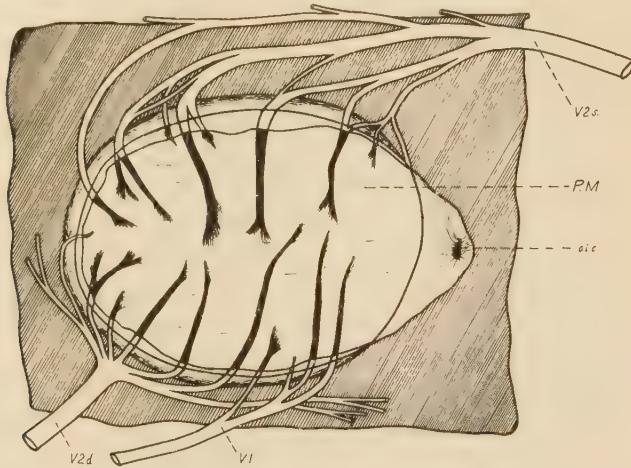


Fig. 9 Dissection of the facial pit. The pit with some of the surrounding skin has been dissected away from the maxillary bone and is represented as pinned, skin down, in a dissecting dish. The inner wall of the inner chamber has been removed so as to expose the pit membrane to view. The nerves ending in the membrane are shown in black for purposes of contrast. *V1*, ophthalmic branch of the trigeminal; *V2s.*, superficial branch of the superior maxillary branch of the trigeminal; *V2d.*, deep branch of the same; *P.M.*, pit membrane; *o.i.c.*, opening of the inner chamber to the exterior.

the nerve fibers to be connected; West ('00) gave a somewhat more detailed description of these nerve endings. Each of these workers, however, had available only a few poorly preserved specimens, and their conclusions were therefore inaccurate and incomplete with respect to a number of important points.

In the present investigation microscopical preparations of the pits of both adult and embryo snakes have been used, for,



while a study of the adult tissues is essential for forming a correct idea of the histology of the organ, many important features are best investigated by an examination of late embryos. In these, decalcifying methods (which, when used, unavoidably produce some distortion) are not necessary and consequently much better sections can be obtained. For general work various fixation methods were used; adult tissues were fixed in aceto-formol and in Bouin's fixing fluid, while chrom-aceto-formalin fixation proved especially useful for embryos. A number of staining methods were found to be of value for bringing out different features and the following were employed with good results: Flemming's tricolor stain, Heidenhain's iron haematoxylin, Ehrlich's triple stain, and Delafield's haematoxylin followed by counterstaining with aqueous eosin. In embryos a good differentiation of tissues was obtained by fixation in Bouin's fluid followed by staining with Mallory's triple connective-tissue stain. The material after fixation was embedded in paraffin, sectioned, mounted, and stained on the slides. For bringing out nervous tissue and end organs the methods employed were the gold-chloride method in combination with sublimate-osmic fixation as described by Küpfer ('16, p. 92) and a variation of Boule's modification of the Cajal silver-nitrate technique as used by Hess ('25).

The histology of the skin of reptiles has been subjected to investigation by a number of workers, notable among whom are Leydig ('53, '57, '72, '73, and '76), Kerbert ('76), Batelli ('80), and Cartier ('72). As is well known, these investigators and others have found that the entire surface of the body of snakes is covered by a corneous cuticular layer which is secreted by the cells of the epidermis. The animals undergo frequent ecdyses and at such times this outer layer is shed, usually in a single piece. If, now, one examines the cast 'skin' of a pit viper, it is readily seen that the cuticle extends into and completely lines the pit and also lines the cavity beneath the pit. The lining of this internal cavity appears in the 'cast' as a bag projecting inward from the

corner of the eye.<sup>3</sup> In a shed skin, of course, this bag shows no connection with the lining of the pit proper, and it was this fact which led Russel and Home into the error of representing and describing the inner cavity as a distinct organ and not as an integral part of the pit organ, for their description of the cavity was based upon the examination of its cuticular lining as it appears in the 'cast.'

In sections through the pits of adult snakes the cuticular layers just mentioned are clearly seen (figs. 18 and 20). That which lines the pit (*o.c.*) is quite smooth, like that lining the surface of the scales. The cuticle on the walls of the inner cavity, however, has its surface studded with many rounded tubercles, so that in section it presents a scalloped appearance. This type of sculpture is also found on the body, in the cuticle lining the portions between the scales. The tuberculation is caused by the fact that the epidermal cells in these regions have rounded upper surfaces which project outward as shown (fig. 10); each tubercle thus represents a single cell.

In the adult the pit membrane is made up of but four layers of cells and, since it is unpigmented, is quite transparent. In it run many nerve trunks which branch repeatedly, as previously described, and finally end in the sensory cells to be discussed below. Accompanying the nerves are small blood vessels which originate as branches of the ophthalmic artery; these break up into many capillaries and thus richly supply the membrane with blood. These and other features are best seen in sections through the pits of adult animals (fig. 10). The outer cellular layer of the pit membrane is made up of simple columnar epidermal cells which are essentially like those of the scales of the rest of the body. Interspersed among them, however, are many sensory nerve cells which are evidently ectodermal in origin and which are continuous with the nerve fibers. They are somewhat elongated cells containing rounded nuclei and are best seen in silver-nitrate

<sup>3</sup> It may be remarked here that the presence of such a lining on the walls of the inner cavity furnishes an indication that these walls are of rather late ectodermal origin—a conclusion which is confirmed by embryological study.

and gold-chloride preparations. West ('00) has described them as showing a much-branched appearance, but this is not evident in any of the sections that have been studied. The cytoplasm has a characteristic hyaline appearance and takes

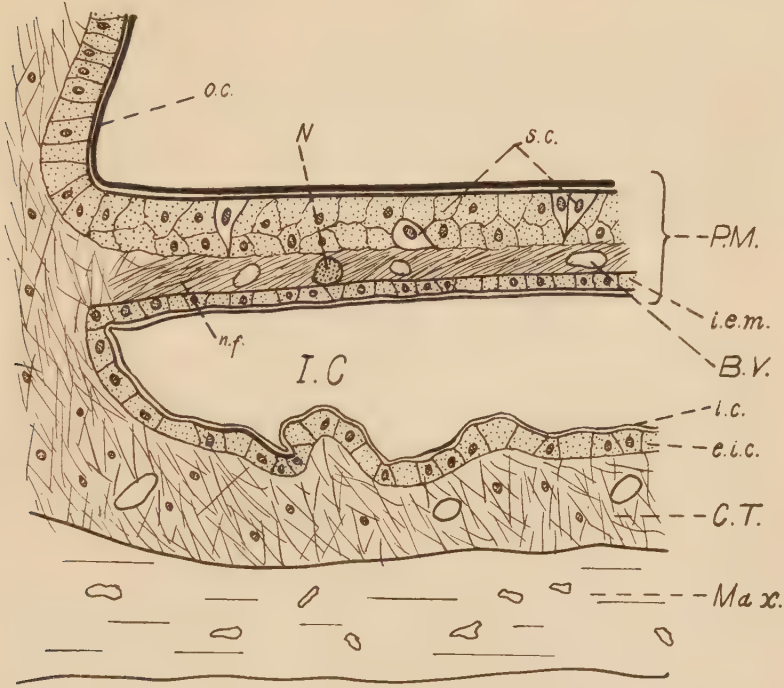


Fig. 10 Drawing of a cross-section through the pit organ of an adult snake (*Agkistrodon mokasen*) to show cellular structure. *C.T.*, connective tissue; *B.V.*, blood vessel; *e.i.c.*, epidermis of the floor of the inner cavity; *I.C.*, inner chamber of the pit organ; *i.c.*, cuticle lining the inner chamber; *i.e.m.*, epidermis of the inner wall of the pit membrane; *Max.*, maxillary bone; *N.*, nerve, in section; *n.f.*, nerve fibers; *o.c.*, cuticle lining the outer chamber of the pit organ; *P.M.*, pit membrane; *s.c.*, sensory cells.

the stain only very weakly. The cells are quite large (10 to 15  $\mu$ ) and vary considerably in form, as shown in the figure (fig. 11).

Beneath the epidermal layer, there is a very thin layer of connective tissue in which run the nerve fibers and blood



vessels. In the embryonic stages, this layer is quite thick, but as development proceeds it becomes increasingly thinner until in the adult it is no more than two or three cells deep.

Finally, the inner wall of the pit membrane is made up of the small cuboidal cells which secrete the cuticular lining of the inner cavity. The cuticle in that region is not so pronouncedly tuberculated as is that which lines the rest of the inner cavity, although a slight scalloped appearance is always noticeable even here. In the adult, in addition to the tuberculations present, the inner and side walls of the inner cavity are thrown into a large number of folds, the surface

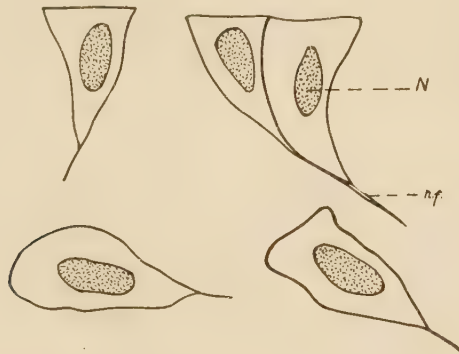


Fig. 11 Camera-lucida drawings of typical sensory cells of the pit organ. *N.*, nucleus; *n.f.*, nerve fibers.

being thereby greatly increased. The cells lining these walls are epidermal cells which are similar to those of the general body surface, but are somewhat shorter, so that instead of being columnar they approach the cuboidal type. They have prominent spherical nuclei. Between these cells and the maxillary bone is a loose, irregularly arranged connective tissue which becomes considerably denser as it approaches the bone. A number of blood vessels and a few small nerves are present in this layer also.

All of the above features may be observed in sections of adult pit organs, but as has been mentioned, a number of details of structure are best seen in very late embryos in which the hard cuticle is not yet formed. It must be borne in mind,

however, that the organ does not reach its full development until much later—some time after birth. Thus in an embryo just before birth the pit membrane is much thicker than in the adult (figs. 15, 16, and 21), but the same cell layers are distinguishable. The external layer is made up of columnar epidermal cells, none of which seem as yet to be noticeably differentiated as receptors. The connective-tissue layer beneath this is comparatively thick and is responsible for the greater thickness of the membrane in the embryo. Blood vessels may be seen to enter the membrane and run in this layer, and the main nerve branches are easily distinguishable (figs. 16 and 21). The surface of the inner cavity of the pit organ in the embryo is quite smooth, showing nothing of the tuberculation which is so striking in the adult tissue.

#### EMBRYOLOGICAL DEVELOPMENT OF THE FACIAL PIT

In order to learn something of the embryological development of the pit organ, a study has been made of sections of the heads of embryos of the copperhead (*Agkistrodon mokasen*) and of the water moccasin (*Agkistrodon piscivorus*). The former were fixed either in Bouin's fixing fluid or in chrom-aceto-formol, the latter were all fixed in Bouin's. They were sectioned at  $10\mu$  and stained on the slide with Delafield's haematoxylin and aqueous eosin.

The only mention in the literature of the embryology of the pit organ is that made by West ('00), who was able to ascertain that the outer and inner chambers both arise by invagination of the ectoderm. His material was, however, inadequate for any detailed study of the processes involved in this development.

In the present study the embryological series was fairly complete and the ontogeny of the organ could be traced from the time of its origin. The smallest embryo obtained was 4 mm. in length. At this stage the sections show no sign of the pit organ, although all other sense organs are well along in their development. In fact, the first evidence of the origin of the pit is found in a much later stage, when the eye with

its lens is well formed. Just anterior to the eye there is at this time a slight depression in the epidermis which represents the beginning of the pit organ and is destined to form the pit proper. As development goes on this depression deepens and at a considerably later stage there arises from its posterodorsal border a second invagination which also becomes deeper and so comes to form a second pit lying behind the first. This is to be the inner chamber of the pit organ. At first its communication with the exterior is quite widely open, but later it closes up, leaving only the small opening found in the adult. This closing over occurs by growth of tissue inward between the two invaginations. In this way the pore by means of which the posterior invagination communicates with the outside comes to be at some distance from the external opening of the pit proper, and incidentally, in the region between the two there is formed the groove which connects the pit with the border of the orbit. This groove is therefore merely a sort of scar marking the place where, during development, the tissue has grown in to separate the two invaginations. This may be made clear by a series of diagrams (fig. 12).

In the embryo the layer of tissue between the pit and the inner cavity is quite thick, but as development proceeds this 'pit membrane' increases in area and becomes much reduced in thickness. As has been noted, however, the extreme thinness of the membrane found in the adult is not attained until some time after the birth of the animal. The layer of tissue separating the inner chamber from the maxillary bone also becomes thinner as development proceeds, the connective tissue becoming somewhat denser. It is not until a late stage of development that the horny cuticle which covers the body of the adult snake appears. At the time of the first appearance of this cuticle the inner cavity still retains a wide communication with the outside and the cuticle forms a thin smooth lining on the surface of both inner and outer chambers of the organ. Later, however, the cuticle of the inner chamber shows in section the scalloped appearance so char-



acteristic of the adult, and still later the wrinkling of the walls becomes noticeable.

From what has been said it is clear that the pit organ, both inner and outer portions, is an ectodermal structure arising in a way which is somewhat reminiscent of the mode of devel-

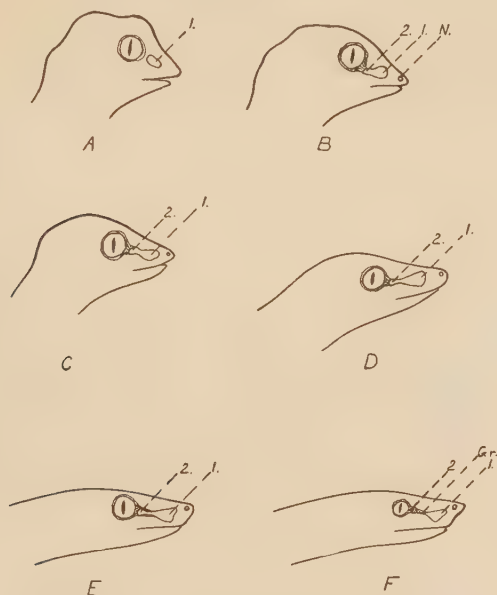


Fig. 12 Diagrammatic drawings of the heads of embryos of *Agkistrodon mokasen* to show successive stages in the development of the pit organ. 1, the primary invagination in the epidermis which later forms the outer chamber of the pit organ; 2, the second invagination, which arises from the posterodorsal border of the first and is destined to form the inner chamber of the pit organ; Gr., the groove in the skin marking the place where the tissue has grown together between the two invaginations; N., nostril.

opment of the vertebrate ear. Moreover, the results indicate, if the time of its appearance in ontogeny is to be considered as of any significance, that this organ is of comparatively recent phylogenetic origin.

#### THE LABIAL PITS OF PYTHONS AND BOAS

Mention has already been made of the fact that certain members of the family Boidae have the labial shields pitted

and that these pits have, by some investigators, been considered as homologues of the facial pits of the pit vipers. Owen (in his "Comparative anatomy," vol. 1, p. 555) implies such an homology, while Gadow ('01) and Ditmars ('10) both attribute to the labial pits a sensory function. The distribution of these pits both anatomically and taxonomically is noteworthy; certain genera show well-marked pits on all of the upper and lower labial shields as well as on the rostral; others, however, have only a few pits, and still others have none at all. In general, it may be said that most snakes of the subfamily Pythoninae have pits on certain of the labial shields, while most of those of the subfamily Boinae have none. This is not an absolute rule, however; for certain genera in both groups are exceptional in this respect, *Loxocemus* among the Pythoninae possessing no pits and *Epicrates* and *Corallus* among the Boinae having them.

The chief reason for postulating a functional analogy between these pit organs and those of the pit vipers is that the two have a similar innervation. The labial pits are richly supplied with nerves, all of which come from the trigeminal, just as do those which supply the facial pits of the Crotalinae. To demonstrate this, figures are given herewith (figs. 13 and 14) of dissections of two snakes, one belonging to the Pythoninae, the other to the Boinae. In these the trigeminal gives rise to the usual three branches: ophthalmic, superior maxillary, and inferior maxillary. The ophthalmic branch, as in other snakes, runs forward inside the skull, penetrates into the orbit, crosses over the optic nerve, and then, reentering the skull, passes above the olfactory nerve and runs anteriorly along its proximal side. In this way it reaches the tip of the muzzle and, in snakes having a pit in the rostral shield, supplies that pit. In those having no pit in the rostral the ophthalmic supplies the general surface of the skin in that region. The pits of the upper labials, be they few or many, are all innervated by divisions of the superior maxillary branch of the trigeminal. This branch divides, as previously described for other forms, into two main

branches, one of which runs superficially just below the eye, while the other is more deeply situated. The superficial branch may be said in general to supply the pits of the posterior labials when these are present; the deep branch supplies those of the anterior labials. This is illustrated by the two specimens figured. In *Python molurus* only the anterior upper labials are pitted and these are supplied by the deep branch of the superior maxillary; this branch after passing behind the eye enters the maxillary bone and runs forward in

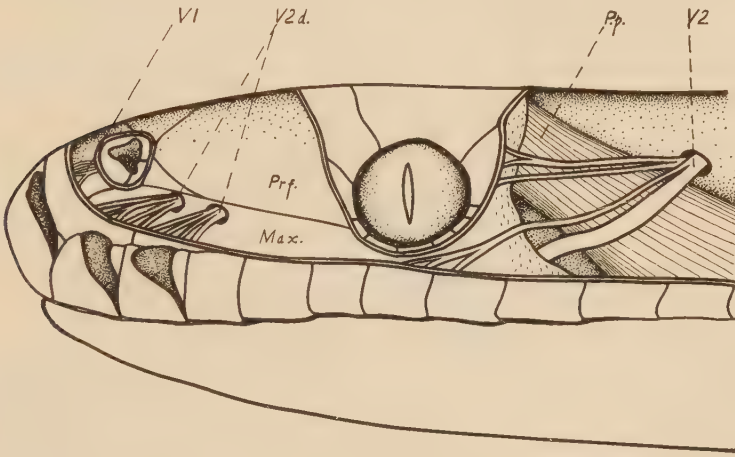


Fig. 13 Dissection of the head of *Python molurus* to show the innervation of the labial pits. Lettering as in figures 4 to 8. *Prf.*, prefrontal bone.

it, sending off branches at intervals. These emerge through special foramina and break up into many small fibers which ramify in the connective tissue beneath the pits of the anterior labial shields. No pits being present in the posterior labials, the superficial branch of the superior maxillary goes to supply the general surface of the skin around the eye and in the roof of the mouth. In the case of *Corallus canina* both anterior and posterior upper labials are pitted. The anterior pits are innervated by the deep branch of the superior maxillary in essentially the same manner as described above; the posterior pits are supplied by the super-



ficial branch. When pits are present in the lower labial shields, as is the case with *Corallus canina*, their nerve supply is derived from the inferior maxillary branch of the trigeminal. This branch emerges from the skull through its own foramen and runs ventrally to penetrate into the mandible. Here it gives rise to two branches, one of which runs forward in the bone and emerges anteriorly to supply the most anterior of the lower labial pits. The other emerges almost immediately through a large foramen and goes to supply the pits of the posterior lower labials. These general

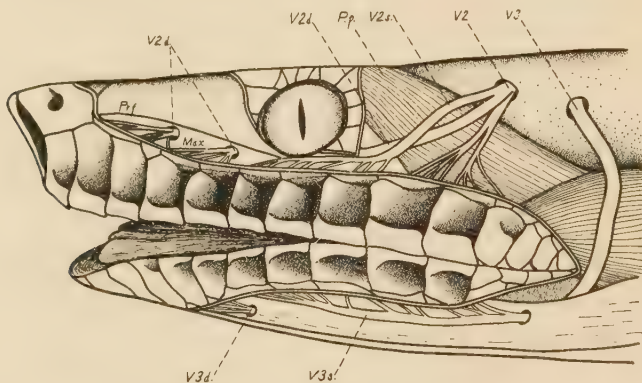


Fig. 14 Dissection of the head of *Corallus canina* to show the innervation of the labial pits. Lettering as in figures 4 to 8. *V3s.*, superficial portion of the inferior maxillary branch of the trigeminal; *V3d.*, deep portion of the same.

rules as to innervation were found to hold for all the snakes of this group which were investigated.

Thus it is clear that, as regards source of innervation, the labial pits of the Boidae are similar to the facial pits of the Crotalidae. This, however, is the only point of resemblance; in their anatomy and histology the two are quite dissimilar. The labial pits are comparatively shallow depressions in the scales; they are never as deep as the facial pits of the pit vipers and are not impressed upon the skeleton of the animal. Moreover, there is nothing comparable to the 'pit membrane' or to the cavity which subtends it. Also, the nerves supplying the labial pits have an ultimate distribution which is

quite different from that of the nerves which supply the facial pits. The floor of the labial pit is made up of a skin exactly like that of the rest of the surface of the scale and beneath this epidermis is a thick layer of closely knit connective tissue. It is in this layer that the nerve branches end, the nerve endings being rather deeply embedded in the tissue.

From these considerations it seems quite clear that if these organs do have a functional similarity to the pit organs of the Crotalidae, the function must be carried out, in the two, in quite diverse ways. In all probability there is no homology here; the superficial resemblance and the functional analogy, if there is one, are wholly the result of convergence.

Unfortunately, there has been no opportunity to obtain any evidence as to the embryological development of the labial pits, although this feature would certainly be most interesting as bearing upon the problem of their possible relation to the lateral-line system of organs.

#### DISCUSSION

All investigators who have studied the subject have maintained that the facial pit must have some important functional significance. The earlier workers inferred that this was the case merely on the basis of the position and anatomical prominence of the organ, but later workers were even more impelled toward such a conclusion when it was found that the pit is furnished with so rich a nerve supply. However, though all agreed that it must serve some important function, the ideas as to the exact nature of that function differed greatly. The various hypotheses that have been advanced may be classified as follows:

1. The pit serves as a means of admitting air to the poison apparatus (Harlan, '35).

2. The pit is of a glandular nature, furnishing some specific secretion (Owen, '66; Brühl, '88).

3. The pit has to do with sensory perception.

- A. The external opening of a sense organ—e.g., nasal opening or external auditory opening (Lacépède, 1789; Wagler, '30).

B. A sense organ in itself. 1) Olfactory in function (Desmoulins, 1824). 2) Tactile in function (Chabanaud, '24, and others). 3) 'Sixth sense' (Leydig, '68). 4) Lateral-line system (West, '00).

Some of these ideas laid no claim to being anything more than likely guesses; they were based on no knowledge of either the anatomy of the pit organ or of the habits of the animal possessing it. Certain workers, however, did have some information as to the structure of the organ, although none of them were in a position to come to any very definite conclusions, since their knowledge of the subject was necessarily fragmentary and faulty. This was due, as has been pointed out, to the difficulty they experienced in obtaining proper material for study.

It will be advantageous now to consider the earlier ideas in the light of the facts brought out in the present work. Obviously, some of the theories must be at once ruled out, for the anatomical relations necessitated by them do not obtain. Thus, since the pit organ has no direct connection with any other organ of the head, either by means of a duct or other opening, we may be sure that it cannot be a nasal opening leading to the olfactory organ, an auditory opening connected with the ear, or an opening connecting the poison gland with the air.

Is there any evidence that it may be of a glandular nature? Owen and Brühl in advancing this idea do not seem to have had any definite basis for their hypothesis, but it may be well to consider it; for, while we are not at all inclined to think of the pit itself as having a secretory function, we might well imagine the inner cavity to serve some such purpose. In fact, if we grant that the organ as a whole is a sense organ, the sensory portion being the pit membrane, it is easy to conceive that the inner cavity may be filled with a fluid secreted by certain of the cells bordering it. But this seems not to be the case. No evidence has been obtained that the inner chamber contains any secretion, even though, with this point in mind, repeated dissections have been carried out on



both anesthetized and freshly killed animals. Moreover, the histological character of the lining of the cavity gives no indication of any glandular nature, for, while there are many depressions and concavities in the wall, these are of the nature of longitudinal folds rather than of gland-like invaginations. It is, of course, difficult to ascertain whether or not, over the surface, unicellular glands are present; but it may be said that none of the cells seem to show the characteristics of gland cells, but are, as has been noted, of the simple cuboidal type with a thin cuticle covering their distal surfaces. Thus the evidence indicates that no part of the pit organ has a secretory function.

We come, then, to a consideration of the theory which ascribes to the facial pit a sensory function. It is clear that there are a number of facts which point toward that conclusion. Chief among these is the rich nerve supply with which the pit is furnished. The character and position of the nerve endings clearly indicate that they cannot be other than receptors, and the number, of them concentrated in this small area leads to the conclusion that the organ must have a function which is comparable in importance to that of the highly evolved sense organs like the eye or ear. But granting that the organ is sensory, we are still but little nearer to the solution of the problem, for as to the exact nature of the sensory function nearly every possible idea has been brought forward. Investigators have suggested that the organ may serve for the perception of olfactory stimuli, of tactile stimuli, of auditory stimuli, or even as an organ of 'sixth sense.' Can our knowledge of the anatomy of the pit organ aid us in solving this difficulty?

The chief exponent of the theory that the facial pit serves in olfaction was Desmoulins (1824). As has been said, he based his idea on the fact that the organ derives a part of its nerve supply from a nerve (ophthalmic branch of the trigeminal) which at the time of his writing was believed by some to function in olfactory perception. This latter theory was subsequently disproved, however. The results of the

present investigation seem definitely to preclude the possibility of the organ's serving an olfactory function. True, it does bear a superficial resemblance to the nostril, since it is a deep invagination in the head. But one of the most essential features necessary for olfaction is wanting; that is, the abundant mucous secretion which must constantly bathe olfactory cells in order that their function may be carried on. For odors to be perceptible by ordinary olfactory cells the chemicals causing them must be dissolved in a liquid which is in free contact with those cells. In the pit organ this requirement cannot be fulfilled. The sensory cells are not covered with mucus, but, on the contrary, have a thick cuticular lining which effectually prevents the admission of moisture. In addition to this, it will be noted that the cells show nothing of the characteristics of olfactory receptors.

Does the pit organ serve as an organ of 'sixth sense' as postulated by Leydig? In his work Leydig has placed in this category a number of tegumental organs which at that time had been but little investigated and whose functions were unknown. Chief among these were the lateral-line organs of fishes and amphibians. These arise as epidermal invaginations and are innervated by branches of the seventh, ninth, and tenth cranial nerves. The sensory cells are in free contact with the water and their function is still somewhat problematical. Some workers believe them to be the seat of a chemical sense, while others regard them as tactile organs functioning in the perception of vibrations and currents in the water. As has been previously stated, Leydig does not seem to have been inclined to regard these as in any way similar in structure to the pit organs of the *Crotalinae*, but he does believe that the two might have similar functions. West, however, implies a true phylogenetic relationship between them, for he speaks of the facial pit as a "tegumental sense-organ of the lateral line series." But a brief consideration of the facts which have been brought out in this paper will serve to show that this idea must be erroneous. The two organs are quite dissimilar in their form, cellular structure,

and innervation. In the lateral-line organ the sensory cells are situated on the floor of a canal which communicates with the surrounding medium by means of small pores, but in the pit organ the sensory cells are situated in a thin membrane which is stretched over an extensive cavity beneath. The lateral-line organ derives its nerve supply from the seventh, ninth, and tenth cranial nerves, while the innervation of the pit organ comes exclusively from the fifth cranial nerve. Thus, if we are to consider the two organs as homologous, we must assume that one of them during the course of evolution has acquired an entirely new innervation—an assumption which is of course scarcely justifiable. Yet another striking difference between the two organs is their embryological development. This feature has been worked out quite extensively for the lateral-line organ in a number of different forms and a good account of this work has been given by Escher ('25). It will not be necessary here to enter into any detail on the subject; it will suffice to say that the developmental features of the lateral-line organ are quite striking and do not in any way resemble those which have been described for the pit organ. Thus the two seem to be in no way related, but have evidently had quite distinct phylogenetic origins.

This does not, of course, obviate the possibility that the pit organ may serve as an organ of a 'sixth sense' the nature of which we do not know and can never know. Such a conclusion is, however, to be avoided, if possible, for it is an hypothesis of the type for which no sure evidence can ever be obtained.

Let us turn rather to a consideration of another of the known sensations. There remains the possibility that the organ may function in the perception of some form of mechanical stimulation; that it may be adapted for receiving tactile stimuli or else for the perception of air vibrations, thus acting like an ear. It seems strange that this theory has been advanced by only a very few of the workers on the subject. One of those who has adduced some evidence tending



toward such a conclusion is Chabanaud ('24). The belief has long been current in our western states that a rope of plaited horsehair, if it is stretched on the ground in the form of a circle, will effectively protect anyone within the circle from the approach of rattlesnakes, and the device is often used by those who find it necessary to sleep in the open in regions where those snakes abound. Since the rattlesnake is a pit viper, the idea has been advanced that perhaps its refusal to cross such a barrier may be a response to tactile stimulation in the region of the facial pit. Chabanaud, at the Ménagerie des Reptiles in Paris, has performed some experiments in order to ascertain whether or not this belief has any foundation in fact. The snakes used were: *Python molurus* (L.), *Tropidonotus natrix* (L.), *Tropidonotus tessellatus* (Laur.), *Vipera aspis* (L.), *Cerastes cornutus* (L.), and *Trimeresurus neuwiedi* (Wagler). A horsehair rope was stretched across the cage of each reptile and observations were made to ascertain whether it would refuse to cross over. Briefly, the result of the experiment was that *Python molurus* and one specimen of *Cerastes cornutus* showed a marked hesitancy to pass over the rope whenever their muzzles came in contact with it. The snakes of the other species seemed quite unaffected. *Python molurus* is, of course, the possessor of labial pits, but *Cerastes cornutus* has neither labial nor facial pits. As Chabanaud remarks, the small number of animals used and the conditions of the experiment make it impossible to draw any conclusion whatever. Certainly there is no indication that the pit vipers show any particular sensitivity to this type of stimulation, for *Trimeresurus neuwiedi*, the only crotaline snake used, seemed utterly oblivious to the presence of the rope and passed over it without hesitation. We would, in fact, hardly expect the pit organ to function in the perception of tactile stimuli. It is ill adapted for such a purpose, because of the fact that the sensory tissue is invaginated and does not readily come into contact with surrounding objects. Even were these snakes to show a marked sensitivity to tactile stimulation in the region of the pit, we would still not be

justified in concluding that the perception of such stimuli is its chief function, for it is well known that important sense organs which are so richly supplied with nerves are usually secondarily sensitive to mechanical stimuli.

A much more likely sensory function and one for which the anatomy of the organ seems well adapted is that of perception of air vibrations. Dr. G. K. Noble, in a recent number of *Natural History* (1930), briefly mentions some experimental work in progress at the American Museum, which seems to indicate that such is the function of the facial pit. Doctor Noble believes that the pit serves for the perception of air vibrations of low frequency and thus aids the snake in directing its strike. The experiments on which this hypothesis is based have not yet, so far as is known, been published. However, from the anatomy alone it seems justifiable to conclude that, among the known senses, this is the one for which the organ is best adapted. But if this is the case, it is obvious that here this function is carried out in a quite different way from that in which it is performed in any other vertebrate auditory organ. For the vertebrate ear has an entirely different structure and method of operation. In it, the air vibrations are received by a tympanum and are communicated by means of the ossicles to the fluid of the inner ear. It is here that the sensory cells are situated. They are affected, through accessory tissue, by the vibrations in the fluid. In the pit organ, on the other hand, the sensory cells are located in the pit membrane, a part which is comparable to the tympanum of the ear. These cells are not surrounded by fluid and have no accessory tissue to transmit the vibrations. Thus, while the pit may have a function which is similar to that of the ear, there can be no analogy between the sensory mechanisms of the two.

There is, however, another auditory organ which, in its structure, does bear a striking resemblance to the facial pit. This is the chordotonal organ of some insects. In certain katydids Hensen ('66), Graber ('82), and others have described an auditory apparatus which consists essentially of

a large trachea lying close under the outer cuticle of the limb. This cuticle becomes thin over an ellipsiform area just above the trachea and a tympanum is thus formed. Since the trachea itself is formed by invagination of the epidermis, it is lined with a chitinous cuticle just as is the outer surface of the body. The tympanum of the chordotonal organ thus consists of two layers of cuticle, the outer layer being that of the outer surface of the limb and the inner layer being the cuticle of the trachea. Between the two are two layers of simple epithelial cells, among which the sensory cells occur. The similarity in structure of this tympanum to the pit membrane will, of course, be clearly recognized. The sensory cells of both organs are evidently of ectodermal origin and in the chordotonal organ they are known to be of two kinds, the two having arisen, it is supposed, one from the epidermis of the trachea, the other from that of the limb. These cells are clearly connected with nerve fibers and they exhibit a unique and complex structure. We have, of course, no wish to imply that there is any homology or genetic relationship between the chordotonal organs of insects and the preorbital pits of snakes, but the structural similarity between the two is worthy of remark, and it seems clear that if the chordotonal organ is able to function in sound perception (as it has been proved to do), then it is certainly conceivable that the facial pit may also be capable of performing such a function. This is, in fact, the idea which the author, purely on the basis of the structure of the organ, is most inclined to view with favor. It is often stated that snakes in general are probably very deficient in the sense of hearing. This is due to the lack of both outer ear and tympanic cavity and to the peculiar arrangement of the columella, which, being in contact with the quadrate bone, is assumed to transmit vibrations to the inner ear with every motion of the quadrate during swallowing. This being the case, we may consider the phylogeny of the pit organ as a second evolution of an auditory organ, providing the crotaline snakes with an ability for sound perception which is not shared by other ophidians. On the basis



of this hypothesis all of the unusual structural peculiarities of the organ are explainable: the pit membrane, acting as a tympanum; the inner cavity, acting as an air chamber; and the pore by means of which that cavity communicates with the exterior, serving to maintain a uniformity of pressure inside and outside. The sensory cells, located in the membrane, may be able to perceive vibrations either by direct action of those vibrations on the cuticle or by the motion of the membrane as a whole which would produce differences in the stresses on the various cells.

However, although this is indicated by the evidence thus far obtained, it must as yet be considered as of a hypothetical nature. Obviously, if the pit vipers do have an unusual sensitivity to auditory stimuli, we would expect this to be reflected in their behavior or habits, but thus far no indication of this has been noted in the literature. This is not very surprising, however, for our knowledge of the natural habits and reactions of even the most common snakes is very fragmentary and we know even less with respect to the poisonous species. If our hypothesis is correct, we should also expect striking differences between crotaline snakes and others in their reactions to auditory stimuli experimentally applied. And it is upon work on this subject that the final decision as to the function of the organ must rest. Unfortunately, there is nothing whatever in the literature bearing on this problem. Manning ('23) has given us some notes upon the hearing of rattlesnakes, but the experiments were not controlled by comparing the auditory ability of these reptiles with that of pitless snakes. Admittedly, snakes are by no means easy to work with experimentally, due to the frequent inhibition of reactions, and this is especially true of the poisonous forms. Nevertheless, they would certainly repay extensive physiological investigation with respect to this problem. Some work of this nature has already been done by the author and the experiments are still in progress.

## SUMMARY AND CONCLUSIONS

The facial pit is a rather complex organ consisting of two chambers separated from each other by a thin sheet of tissue, the 'pit membrane.' The outer chamber is widely open and is in free communication with the air; the inner chamber communicates with the exterior by a small pore situated near the anterior border of the orbit. The cuticle which covers the body extends into this inner chamber and there presents a much-tuberculated appearance, the tuberculations being most pronounced in adult specimens. The 'pit membrane' is richly supplied with nerves derived from the ophthalmic and supramaxillary branches of the fifth cranial nerve.

Histological study shows that the nerve fibers are continuous with large sensory cells which are characterized by their hyaline cytoplasm and large rounded nuclei. These cells are richly distributed in the pit membrane, usually being found among the epidermal cells, from which they are evidently derived.

The cells lining both inner and outer chambers of the pit organ are ectodermal in origin. They show no sign of being of a glandular nature.

The pit organ originates rather late in development, first appearing as a slight invagination of the epidermis just anterior to the eye. This depression gradually deepens and later another invagination makes its appearance near the posterodorsal border of the first. The first of these forms the pit proper, while the second comes to lie behind the other, so as to form the inner chamber. In the embryo the layer of tissue between the inner and outer chambers of the pit organ is quite thick, but as development proceeds it becomes much reduced in thickness and forms the 'pit membrane' of the adult.

The labial pits of pythons and boas, although they are innervated by the same nerves as are the facial pits of the pit vipers, have been found to differ markedly from the latter with respect to form and cellular structure, and the indication is that the two are in no way homologous.

On the basis of the facts brought out in the present study, a number of the earlier theories as to the function of the facial pit seem to be definitely eliminated, for they demand certain peculiarities of structure which do not obtain.

In its structure the organ under consideration shows certain very striking resemblances to the chordotonal organ of insects, an organ which is known to be auditory in function. The pit organ, it would seem, is structurally well adapted to perform a similar function. It is innervated by a nerve which, in other snakes, is known to supply tactile end organs. The pit organ may represent a concentration of that function. The pit membrane, in which the end organs are located, is stretched tightly over an air-filled cavity and so is well suited to function in the perception of a certain type of tactile stimuli, namely, air vibrations. That the pit organ actually does function as a receptor for such stimuli, however, remains to be proved by experimental methods.

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## PLATE 1

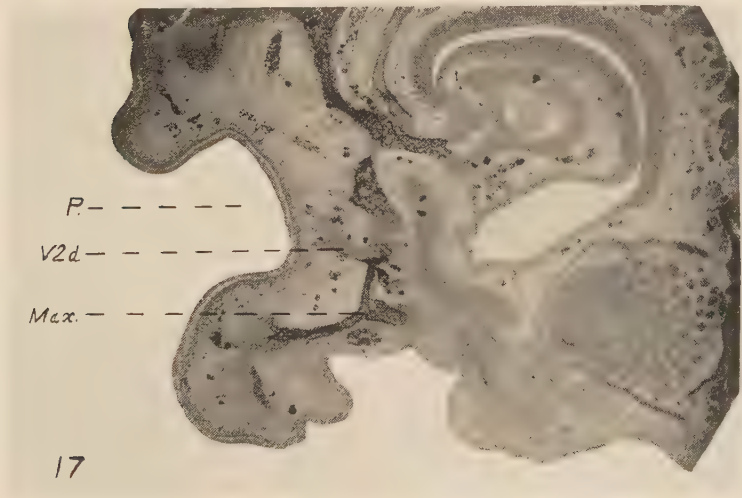
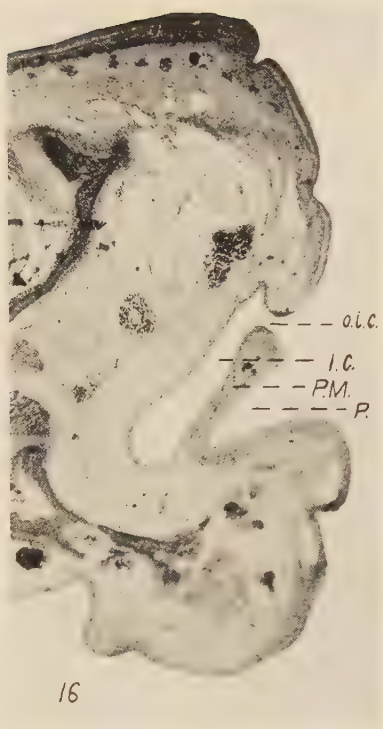
### EXPLANATION OF FIGURES

15 Section through the head of a late embryo of *Agkistrodon mokasen*.  $\times 75$ . Mallory's triple connective-tissue stain. *P.*, pit; *I.C.*, inner chamber; *P.M.*, pit membrane; *o.i.c.*, external opening of inner chamber; *Max.*, cartilaginous anlage of maxillary bone.

16 Section through the head of a late embryo of *Agkistrodon mokasen*.  $\times 75$ . Mallory's triple connective-tissue stain. Lettering as above.

17 Section through the head of a late embryo of *Agkistrodon mokasen*.  $\times 75$ . Mallory's triple connective-tissue stain. Lettering as above. *Vzd.*, deep portion of the superior maxillary branch of the trigeminal nerve.





## PLATE 2

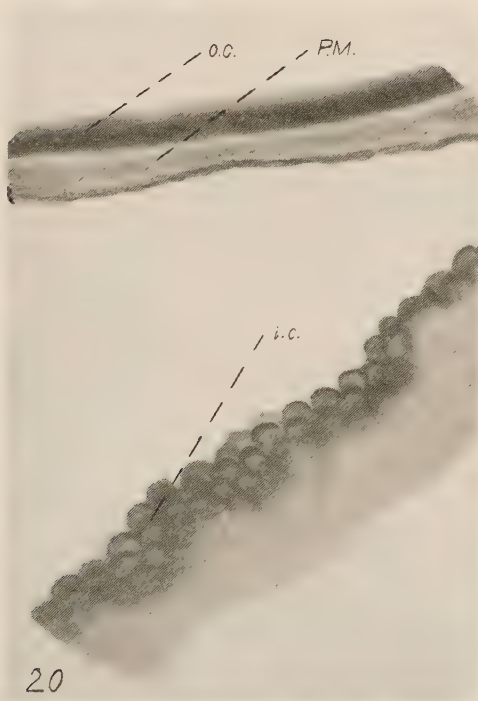
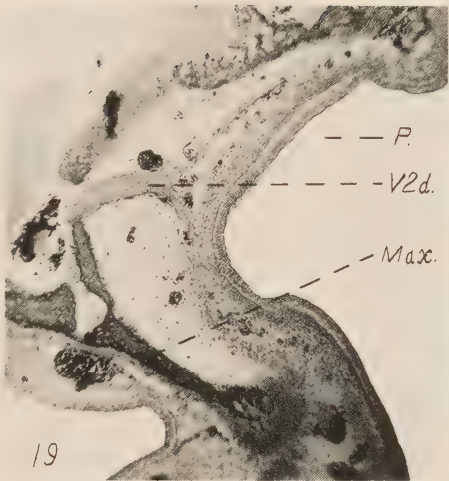
### EXPLANATION OF FIGURES

18 Section through the pit organ of an adult snake (*Agkistrodon mokasen*).  $\times 75$ . Silver-nitrate technique. *o.e.*, cuticle of the outer surface of the pit membrane; *i.e.*, cuticle of the inner chamber; *P.M.*, pit membrane.

19 Section through the pit organ of a late embryo of *Agkistrodon mokasen*, showing the penetration of the deep portion of the superior maxillary branch of the trigeminal through the maxillary bone.  $\times 120$ . Mallory's triple connective-tissue stain. Lettering as in preceding figures.

20 Detail of figure 18.  $\times 350$ .

21 Section through the pit organ of a late embryo of *Agkistrodon mokasen* taken posterior to that shown in figure 19.  $\times 120$ . Mallory's triple connective-tissue stain. Lettering as in preceding figures.







### VITA

W. Gardner Lynn was born at Washington, D. C., December 26, 1905. When he was five years of age, his parents moved to Lonaconing, Maryland, and his elementary education was begun in this town. This education was continued from 1915 to 1919 in Hagerstown, Maryland, and from 1919 to 1921 in Baltimore, Maryland. In 1921, he entered high school, the Baltimore City College, from which he graduated in 1924. In the same year, he matriculated at the Johns Hopkins University and, four years later, received the baccalaureate degree from that institution.

From 1928 to 1931 he was a graduate student in biology at the Johns Hopkins University, being assistant in comparative anatomy during the scholastic year, 1929-1930.

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